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Notes on Micro-Fabric in Upper Paleozoic Scallops

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ABSTRACT

Microstructure of the outer shell layer of upper Paleozoic pectinoid bivalves usually, but not always, is strikingly different in right and left valves, and the differences characterize groups at the generic and familial levels, serving to augment sparse

morphologic characters available for taxonomic and phylogenetic studies. The progress note given here is one aspect of an ongoing comprehensive taxonomic survey of Permian and Lower Triassic Pectinacea.

INTRODUCTION

As part of a comprehensive taxonomic survey and revision of Permo-Triassic scallops (Pectinacea) we present here a preliminary note on the microscopic shell-fabric in comparison with an analogous living scallop. The fieldwork was supported in part by a grant from the National Geographic Society.

More than a half century has elapsed since the Danish petrographer, O. B. Bøggild, showed malacologists the importance of shell microstructure in their taxonomic studies (Bøggild, 1930). His seminal work has been refined by many investigators (see Carter, 1980a, for citations). But this field of investigation has lagged, and very much remains to be done on the taxonomic, environmental, and stratigraphical distributions of the microscopic elements.

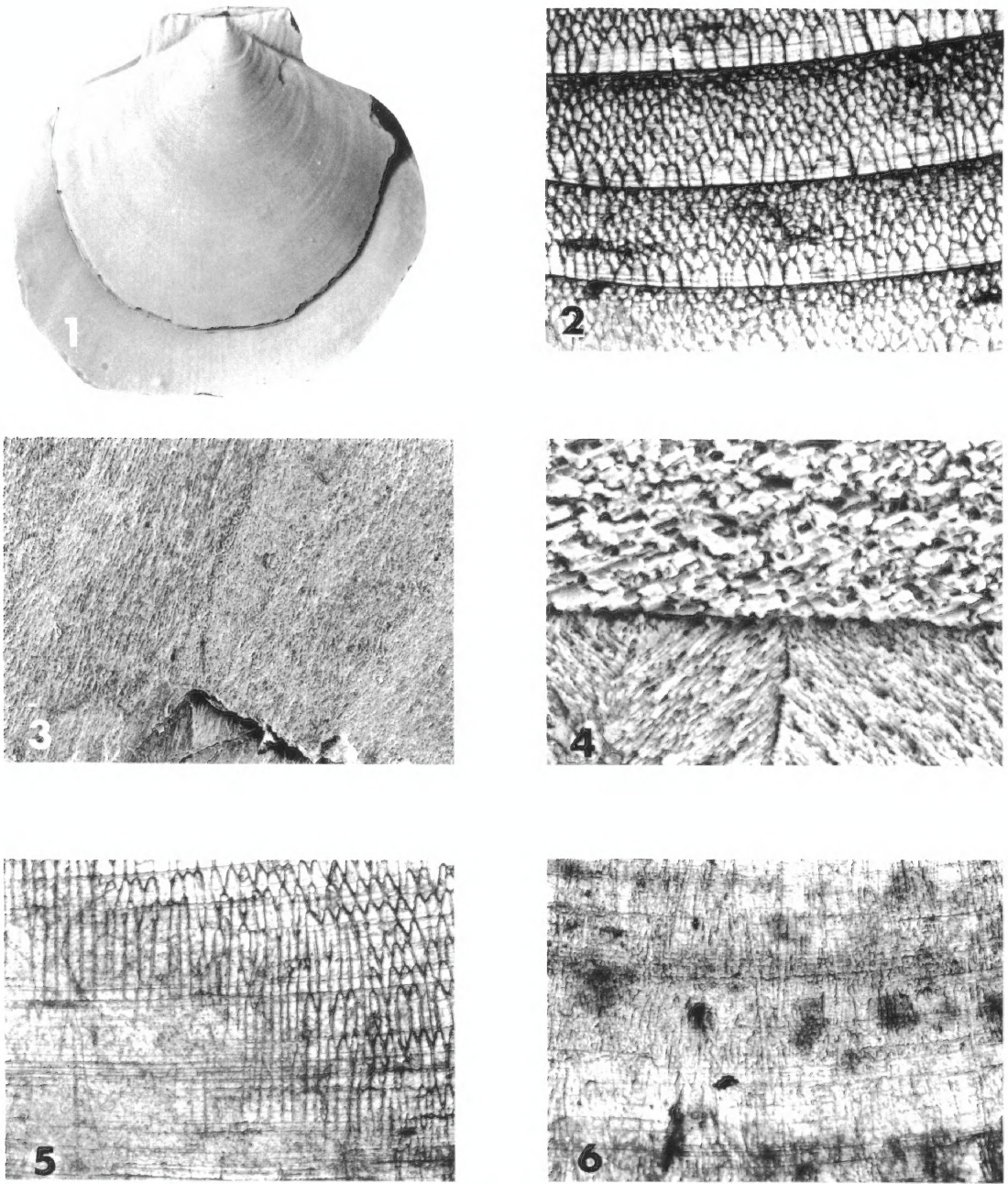
Fossil bivalves display relatively few taxo-

nomic characters under the best conditions of preservation. So inclusion of data on distinctive shell fabrics facilitates discrimination of otherwise similar categories.

The microscopic elements of molluscan shells are composed of calcium carbonate encased in a matrix of proteinaceous material—conchiolin. Since these, both the carbonate and the conchiolin, are chemically unstable, the fossil shells usually have suffered progressive destruction of biological details with increasing geologic age. The conchiolin matrix or the aragonite may disappear first, and this change commonly is followed by recrystallization of the calcite or dissolution of all the calcium carbonate. Any or all the original substances may be replaced by secondary minerals, with or without preserving vestiges of the biologic fabric. Good preservation of

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FIGS. 1-6. *Propeamussium sibogai*, 1. $\times 2$. Right side view. The flexible prismatic apron has broken away from the margin. Recent shell, Japan. AMNH cat. no. L181809. 2. *Propeamussium dalli*, $\times 15$. Outer surface of right valve viewed with transmitted light. Simple inclined prismatic structure. Recent, Cuba. AMNH cat. no. L120931. 3. *Propeamussium dalli*, SEM, $\times 187$. Outer surface of left valve lightly etched. SEM photograph showing radial fibrous prismatic layer over crossed lamellar layer. Beaks toward upper right. Recent, Cuba. AMNH cat. no. L120931. 4. *Propeamussium sibogai*, SEM, $\times 3800$. Left valve. Etched transverse section. Radial fibrous prismatic layer above, crossed lamellar inner layer below. Recent, Japan AMNH cat. no. L181809. 5. *Propeamussium dalli*, $\times 15$. Right valve. Outer surface viewed with transmitted light; transition from simple inclined prismatic structure (above) to radial fibrous structure on posterior ear. Recent, Cuba, AMNH cat. no. L120931. 6. *Propeamussium sibogai*, $\times 15$. Left valve. Outer surface with transmitted light showing radial fibrous prismatic structure near ventral margin. Recent, Japan. AMNH cat. no. L181809.

original or replicated fabric in bivalves is quite scarce in rocks older than mid-Mesozoic, but occasional examples have turned up in the Upper Paleozoic and in rocks as old as Devonian (Carter and Tevesz, 1978).

A few ancient morphological grades are represented among living marine scallops, and these aid in interpretations of ancient shells. An example is the deep water *Propeamussium* (fig. 1) cited by Thomas Waller as "a living relict of the past" (Waller, 1971, 1972). He showed that this pectinoid is much more primitive than other living scallops, and more closely resembles some Late Paleozoic genera such as *Pernopecten* (figs. 8–10). Our examination of several species of *Propeamussium* indicates a need for some clarification of the living genus, and aids in the grouping of the Upper Paleozoic forms.

RIGHT VALVES OF PROPEAMUSSIUM

The fabric in the two valves of *Propeamussium* is discrepant, unlike most living scallops in which both valves are alike in being composed almost entirely of foliated calcite. Waller (1972) has shown that the valves of *Propeamussium* are multilayered. The right valve possesses a thin outer layer (ectostracum) of short, more or less inclined, simple prisms of calcite (figs. 2, 5, 12), as in many pleurothetic bivalves, unlike the left (upper) valve, in which the much finer prisms

are horizontal and radial (fig. 6). Instead, the outer layer of the left valve was described by Waller as foliated calcite. However, the term "foliated" for this genus is ambiguous, and we prefer Carter's term "fibrous prismatic" (Carter, 1980b, p. 646).

A similar discrepancy between right and left valves is usual among upper Paleozoic pectinoids, especially in the genus *Pernopecten* (Newell, 1938). Waller made the interesting discovery that the simple prisms in right valves of *Propeamussium* become "foliate" on the ears and upper flanks of the shell (Figs. 5, 7). He also discovered a transition from prismatic to foliate structure in oysters (Waller, 1981), from which he concluded that the foliate structure is derived ontogenetically from simple prisms. In any case, the ontogeny of some modern scallops also indicates that foliate structure may replace the more primitive prismatic structure (fig. 7), a tendency apparently already completed in Permian *Dellopecten* which seems to be entirely foliate (Dickins, 1957).

In *Propeamussium* the prismatic layer of the right valve extends beyond the inner non-prismatic layers as a broad, flexible apron. Dried museum examples of *Propeamussium* (fig. 1) and the distantly related pearl clams (Pteriidae), such as *Pinctada*, usually lose this fragile part of the shell after death, giving an illusion that the right valve is much smaller than the left. One of us originally considered

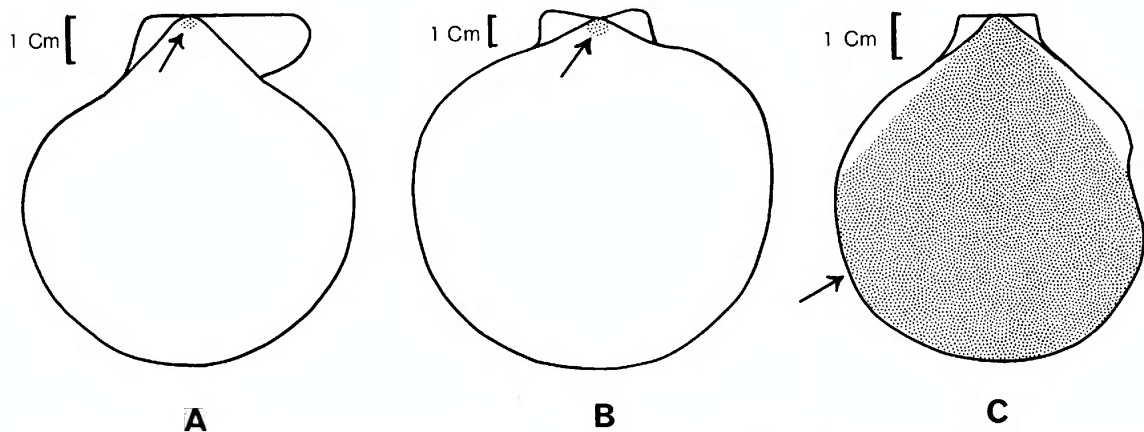
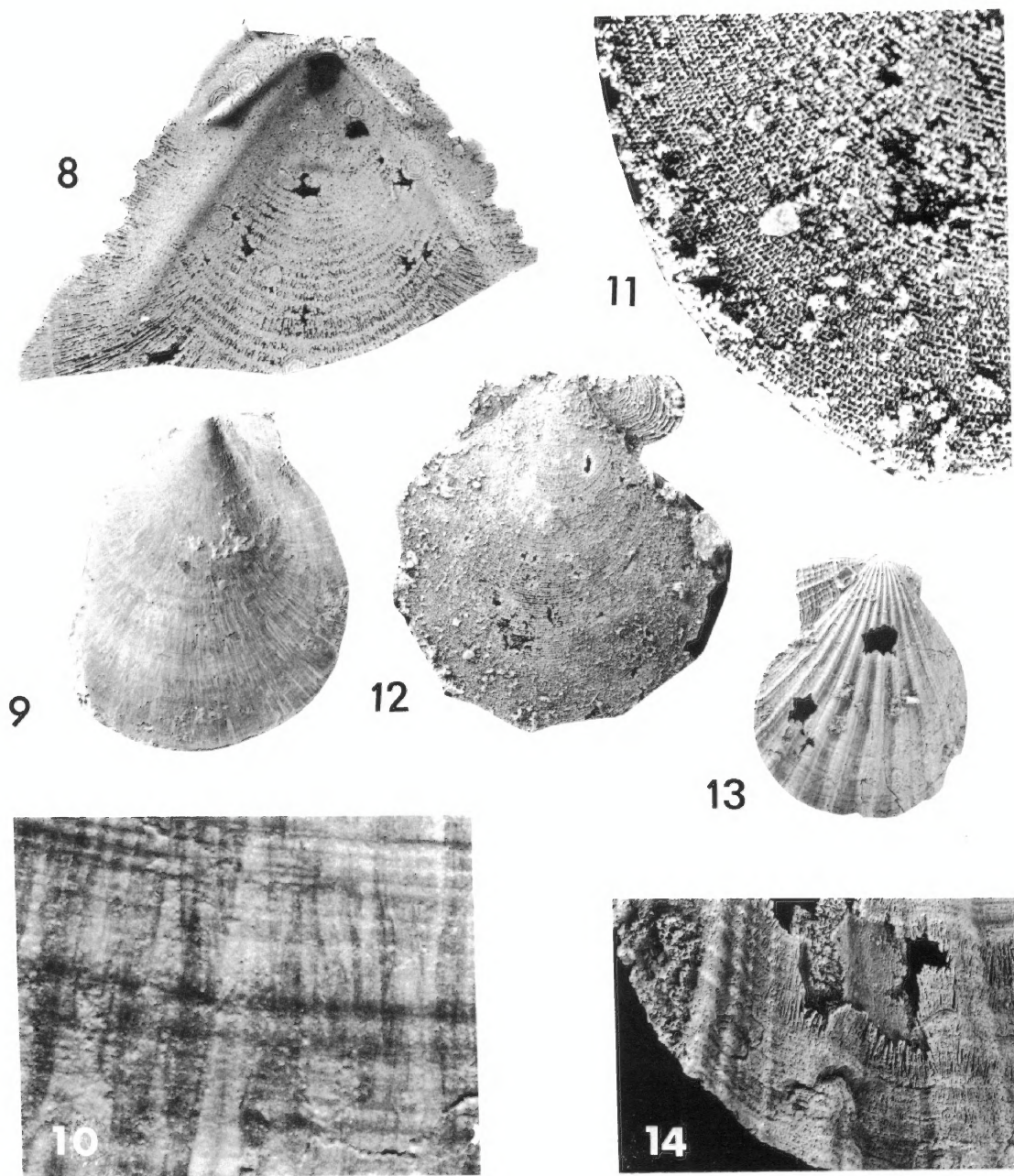


FIG. 7. A–C. Right valves of recent pectinaceans showing variation in the area occupied by the outer prismatic layer (stippled). A. *Chlamys islandica*. B. *Amusium japonicum*. C. *Propeamussium* sp. In the first two, the white areas represent foliate calcite. In the third, fibrous prismatic calcite (from Waller, 1972).



FIGS. 8-14. 8. *Pernopecten* sp. Left valve, $\times 4$. Siliceous replacement. The outer fibrous layer shows where the inner layer has flaked off. Permian Cathedral Mt. formation, USNM loc. 702, cat. no. 382758, Glass Mts., Texas. 9. *Pernopecten* sp. Left valve, $\times 1\frac{1}{2}$. Calcareous shell, showing fibrous structure. Plattsburg Formation, Pennsylvanian, 4 mi. East of Ottawa, Kansas. AMNH cat. no. 42778. 10. Same, $\times 8$. 11. *Euchondria* sp., $\times 15$. Silicified right valve illustrating simple prismatic structure, from the Permian Road Canyon Formation, Glass Mts., Texas. USNM loc. 720d, cat. no. 382759. 12. Same, $\times 5$. 13. *Guizhoupecten* sp., $\times 1$. Silicified left valve showing radial fibrous structure. Lower Getaway limestone, USNM loc. 728, cat. no. 382760, Guadalupe Mts., Texas. 14. Same, $\times 8$.

such valves as "discordant" (Newell and Merchant, 1939). They are not so. Margins of the two valves match perfectly in living specimens.

LEFT VALVES OF PROPEAMUSSIUM

Left (dorsal) valves in most living scallops and pteriaceans are rigid all the way to the marginal commissure. In some of the Paleozoic pectinaceans, the outer calcite layer seems to be homogeneous—without definite biogenic structure (Newell, 1938; see Carter, 1980, for definition). The outer layer of the left valve (fig. 3) is radially fibrous prismatic throughout, and similar radial structure characterizes both valves of several Paleozoic genera (e.g., *Streblopteria*, *Streblochondria*, *Guizhoupecten*, and *Obliquipecten*).

This radial structure resembles the radial prismatic structure of living *Mytilus*. Replicas of radial structure (Boyd and Newell, 1985) are occasionally preserved in silicified specimens of *Pernopecten* and *Guizhoupecten* (figs. 8–10, 13, 14). These tend to be welded and are therefore difficult to characterize. Both left and right calcareous shells of *Streblochondria* from the Pennsylvanian (Newell, 1938, pl. 15, fig. 14a) also have the microstructure of left valves of *Propeamussium*.

The inner ostracum is generally concentric crossed lamellar, or foliate, in pectinoids of the Upper Paleozoic. Additional nacreous layers occur in *Limipecten*. Many genera are not yet properly investigated. Features of the outer shell layer considered together with other morphological characters, to be described later, suggest the following groupings:

	Outer Ostracum	
	Right Valve	Left Valve
Aviculopectinidae		
<i>Heteropecten</i>	prismatic	homogeneous
<i>Etheripecten</i>	prismatic	absent
<i>Acanthopecten</i>	prismatic	homogeneous
<i>Limipecten</i>	prismatic	homogeneous
Dellopectinidae		
<i>Dellopecten</i>	absent	absent
Euchondriidae		
<i>Euchondria</i>	prismatic	homogeneous
Streblochondriidae		
<i>Obliquipecten</i>	radial fibrous	radial fibrous

<i>Streblopteria</i>	radial fibrous	radial fibrous
<i>Streblochondria</i>	radial fibrous	radial fibrous
<i>Guizhoupecten</i>	?radial fibrous	radial fibrous
Propeamussiidae		
<i>Propeamussium</i>	prismatic	radial fibrous
Pernopectinidae		
<i>Pernopecten</i>	prismatic	radial fibrous
Pterinopectinidae		
<i>Dunbarella</i>	prismatic	prismatic
<i>Claraia</i>	prismatic	prismatic

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